

*STREPTOSYLLIS VERRILLI* (MOORE, 1907),  
NEW COMBINATION, LIFE CYCLE, POPULATION  
DYNAMICS AND PRODUCTION FROM A SALT MARSH IN  
SOUTHERN NEW ENGLAND

*Rafael Sardá and Guillermo San Martín*

ABSTRACT

*Streptosyllis verrilli* is a small syllid commonly found in tidal sandy sediments in Great Sippewissett salt marsh. This species has a monotelic reproductive strategy. *S. verrilli* has been identified in the past as *Syllides verrilli* but the presence of enlarged acicula on some anterior parapodia places the species in the genus *Streptosyllis*. The population of *Streptosyllis verrilli* has an annual life-cycle. Reproduction takes place in May-July by the survivors of the last year's recruitment. Recruitment takes place from June to August; then only juveniles from the new recruitment can be observed. Spring values of biomass and density maxima during the year are a function of the last year population size and the winter mortality due to the weather. The mean annual biomass was 0.10 g dry weight m<sup>-2</sup>, mean annual production 0.33 g dry weight m<sup>-2</sup> and the production : biomass ratio 3.27 during the 2-years studied.

All previous references to this species as *Syllides verrilli* were limited to Cape Cod in southern New England (Whitlatch, 1977; Michael et al., 1975; Sanders et al., 1980). *S. verrilli* seems to be an endemic species to this area. *S. verrilli* is an epigamic species (the morphology of the whole animal changes during reproduction). Reproduction in the family Syllidae has been revised by different authors (Garwood, 1991; San Martín, 1984), and two major types of reproductive modifications are evident, based on whether there are morphological changes in the adults during reproduction (in schizogamic species only stolons are produced). *S. verrilli* reproduces only once at 9-10 months, and death follows spawning. This pattern is uncommon in syllids (Garwood, 1991). Most known epigamic syllids revert to a normal morphology and do not die after reproduction. For example, *S. websteri*, a species very similar to *S. verrilli*, found in the Northumberland coast of England, breeds twice during an extended spawning season at the beginning of their third year of life (Garwood, 1982).

Population dynamics in syllids are not well known. There are a few species that have been studied (Daly, 1975 in *Odontosyllis polycera*; Garwood, 1982 in *S. websteri* or Franke, 1980 in *Typosyllis prolifera*). The lack of knowledge is due to the small size of syllids, difficulty in sampling and misidentification.

During studies of the benthic fauna in Great Sippewissett salt marsh (Cape Cod, southern New England) (Sardá et al., in press) we commonly found this small syllid in silty sand sediments. A detailed examination of these specimens reveals that they have enlarged acicula on some anterior parapodia, and therefore must be placed into the genus *Streptosyllis* Webster and Benedict, 1884.

In this paper, we describe the population dynamics of this syllid polychaete over a 2-year period. Furthermore, we present evidence to show that this species belongs to the related genus *Streptosyllis* rather than to *Syllides*.

MATERIAL AND METHODS

More than 300 individuals were collected and specimens have been deposited in the Marine Biological Laboratory (Gray Museum) at Woods Hole (Massachusetts, USA), the "Museo Nacional de Ciencias Naturales" of Madrid (Spain) and the authors' collections.

*Streptosyllis verrilli* is commonly found in creeks and shallow waters near or in salt marshes of Buzzards Bay (Massachusetts, USA) (Moore, 1907; Banse, 1971; Michael et al., 1975; Sanders et al., 1980). It can live up to 5 cm in depth in sandy sediments (Sanders et al., 1980). In Great Sippewissett marsh, located at Buzzards Bay, it occurs in tidal sandy sediments from coarse to medium grain size (0.20–0.38 mm) and it is not found in sediments below 0.12 mm grain size or in coarse beach sediments. It is common in similar substrate in Pleasant Bay at the eastern end of Nantucket Sound (southern New England) (N. W. Riser, pers. comm.).

Samples were collected from 12 sites in the different habitats of the marsh: beach, main channel, sandy small channels and muddy tidal creeks. Three benthic samples were obtained from each sandy site. Two samples were collected by using an Ekman grab (144 cm<sup>2</sup>, 15 cm depth) and a third sample was carried out using corers 33.2 cm<sup>2</sup> in area, 15 cm deep. Samples were fractioned into three depths: 0–5 cm, 5–10 cm and 10–15 cm. Sandy areas of the marsh, inhabited by *S. verrilli*, were sampled monthly from November 1986 to November 1987. These sites were also sampled from May 1988 to September 1988 during the course of a caging experiment. Control data was obtained in this experiment by collecting three monthly samples with the corer.

All samples were sieved through a 0.5-mm screen and preserved in buffered formalin containing Rose bengal stain. The sediment going through the sieve was saved, and an aliquot fraction was examined with a binocular microscope to count and identify the smaller size fraction of the macroinfaunal community. *S. verrilli* was mostly found in the fraction from the 0–5 cm deep layer.

To measure growth and to identify cohorts, the width of a proventriculus setiger was employed as an estimate of size. The relationship between proventriculus setiger width ( $y$  in  $\mu\text{m}$ ) and setiger number ( $x$ ) yield in a linear regression ( $y = 15.683 + 10.772x$ ;  $r^2 = 0.97$ ). The width of this setiger is a convenient measurement of size because it does not change when the animal is fixed by preservatives and grow in the period of gamete production. Setiger measurements were made on all individuals through a binocular microscope using a camera lucida and digitizing tablet (Houston Instrument HiPAD) linked to a computer. Selected individuals from representative size categories were measured, then dried for 48 h at 60°C and weighed. Dry weight (D.W.) was calculated as a regression to proventriculus width (P.W.). The regression was then used to convert the routine measurement to biomass.

The regression between proventriculus width (P.W.) vs. dry weight (D.W.) was computed as:

$$\text{D.W.} = 0.403232 \cdot \text{P.W.}^{2.306097} \quad (r^2 = 0.73; N = 23).$$

An indirect measure of survival was employed to estimate mortality. We know the abundance of successive age groups in the population so we can estimate the mortality between these ages. Production was estimated by summing increases in biomass that occurred from one sampling date to the next. A second estimate of production was calculated by the equation (1) (Banse and Mosher, 1980) using mean adult size converted to its caloric equivalent ( $M_s$ ) by the taxon specific energy content given in Brey et al. (1988).

$$(1) \quad \text{P/B} = 0.64 \cdot M_s^{0.37}$$

## RESULTS AND DISCUSSION

Family Syllidae Grube, 1850

Subfamily Eusyllinae Rioja, 1925

Genus *Streptosyllis* Webster and Benedict, 1884

*Streptosyllis verrilli* (Moore, 1907), new combination

*Syllides verrilli* Moore (1907): 448–451, figs. 1, 2. Banse (1971): 1475–1476, fig. 4.

*Syllides setosa* Pettibone, 1963: 126, not *S. setosa*, Verrill, 1882.

**Material Examined.** — The description is primarily based on one preserved complete, mature male, epitokous specimen, 3 mm in length, 0.5 mm in width, 28 setigers, but we examined many other specimens out of a collection of more than 300.

**Description.** — Body is relatively short and broad, especially in mature specimens, with a small number of setigers without color marking (Fig. 3). Prostomium subpentagonal with rounded margins; four large, lensed, red eyes in open trapezoidal arrangement and two smaller, anterior eyespots. Antennae short, club shaped, slightly thickened subdistally; median antenna somewhat longer than prostomium, between posterior eyes, lateral antennae shorter than median one, the two

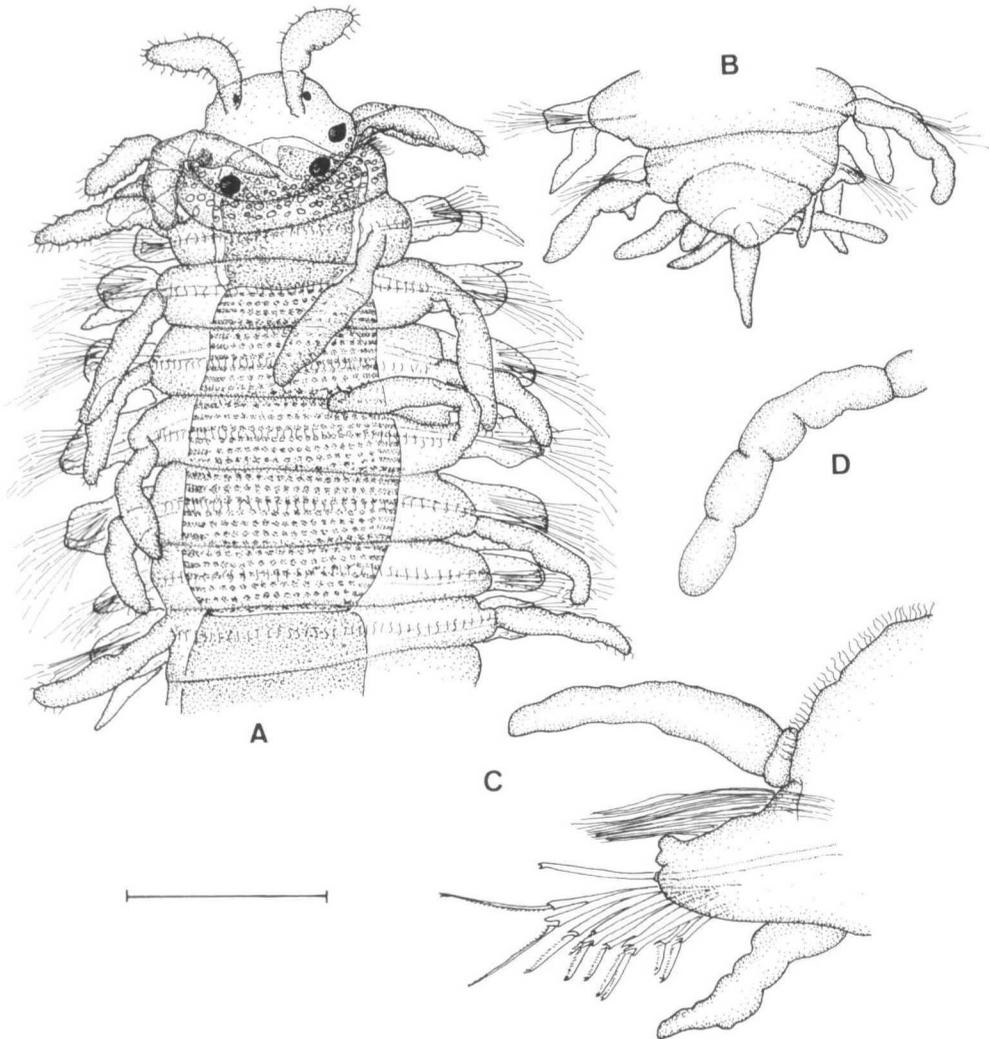


Figure 1. *Streptosyllis verrilli* (Moore, 1907). A) anterior end, dorsal view of a mature, epitokous male. B) posterior end of the same. C) medium parapodium, lateral view, of the same. D) pseudoarticulate dorsal cirrus, 6th setiger. Scale bar: A, B) 0.13 mm. C, D) 0.64 mm.

eyespot at the baseris (Fig. 1A). Palps very small, reduced to two frontal minute papillae (Fig. 3<sub>2</sub>). Peristomium well defined, with some bright golden inclusions, some of them extending dorsally to prostomium (Fig. 1A); two pairs of tentacular cirri, dorsal pair similar to lateral antennae both in length and shape, ventral pair somewhat shorter (Figs. 1A, 3<sub>2</sub>). Two lateral heavily ciliated nuchal organs (Fig. 1A). Segments well defined, with a dorsal ciliary band on each segment (Figs. 1A, 3<sub>4</sub>). Dorsal cirri on all parapodia, rough, relatively short, similar to antennae and tentacular cirri, but less thickened subdistally, nearly twice length of parapodial lobe, with a marked basal cirrophore (Fig. 1C). Occasionally, some dorsal cirri with constrictions, giving a pseudoarticulate appearance (Figs. 1D, 3<sub>4</sub>). Antennae, tentacular cirri and dorsal cirri ciliated, especially distally (Fig. 1A). Parapodia conical, with two distal dorsal papillae (Figs. 1C, 3<sub>2</sub>, 3<sub>5</sub>); a tuft of cilia under parapodial papillae, only perceptible under high magnifications (Fig. 3<sub>5</sub>). Ventral

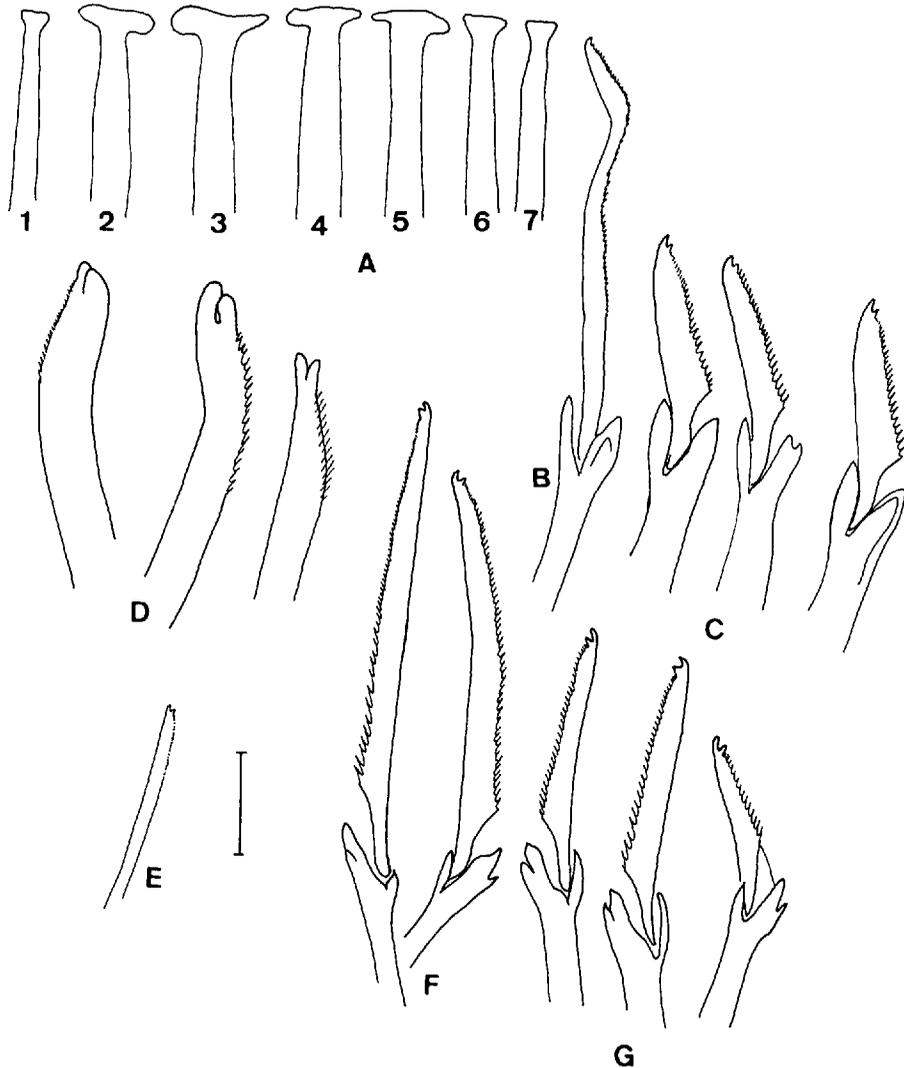


Figure 2. *Streptosyllis verrilli* (Moore, 1907). A) acicula of each first seven right parapodia. B) compound spiniger-like seta, anterior setiger. C) compound falciger setae, anterior setiger. D) dorsal simple seta, different views. E) ventral simple seta. F) compound spiniger-like setae, posterior setiger. G) compound falcigers. Scale bar 10  $\mu$ m.

cirri broad at base, conical distally, rough to pseudoarticulate, longer than parapodial lobes (Fig. 3<sub>3</sub>). Single aciculum in each parapodium, knobbed distally; acicula of setiger 2, 3, 4 and 5 strongly thickened, acicula of setiger 6 less thickened than those of setigers 2–5 but thicker than the rest of setigers (Fig. 2A). Compound setae hemigomph, with a thick, subdistal spine, oriented on an oblique, different angle than tip of hinge. About 15 compound setae in each anterior parapodium (first six setigers); three upper long spiniger blades with short spines on cutting margin, minutely bidentate (Figs. 2B, 3<sub>3</sub>), 12 lower falciger blades, with somewhat longer spines on cutting margin, bidentate with small proximal teeth (Fig. 2C). Remaining parapodia each with about similar compound setae distinctly bidentate, 2 of them spiniger-like, about 50  $\mu$ m long (Figs. 2F, 3<sub>8</sub>) and 8 falcigers, 27

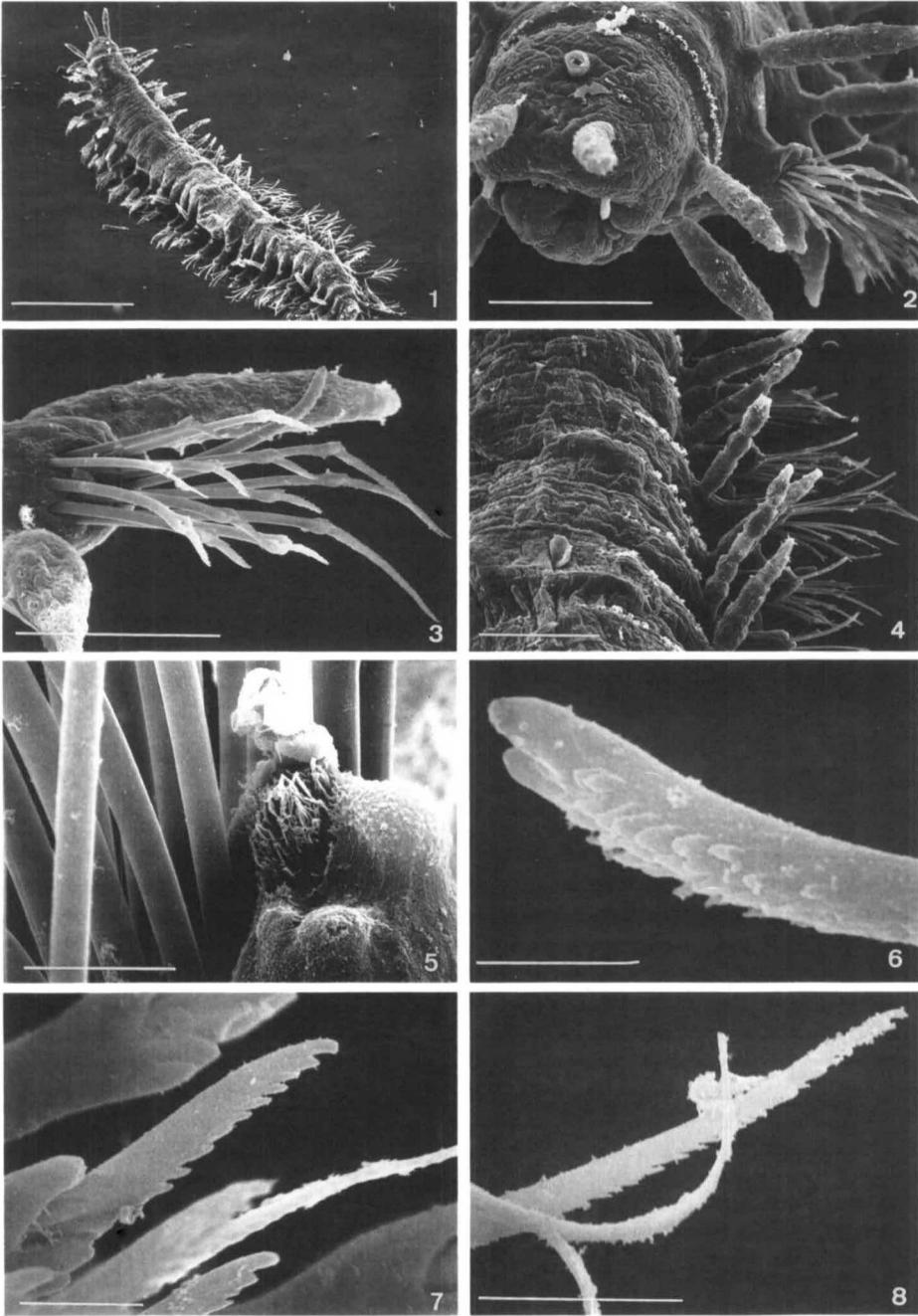


Figure 3. *Streptosyllis verrilli* (Moore, 1907). 1) General view. Scale bar, 500  $\mu\text{m}$ . 2) Detail of the anterior end, dorsal view, showing the lateral and median antennae and the two small palps reduced to frontal minute papillae. Scale bar, 100  $\mu\text{m}$ . 3) Anterior parapodia. Scale bar, 50  $\mu\text{m}$ . 4) Dorsal cirri with constrictions and ciliary band in each segment. Scale bar, 100  $\mu\text{m}$ . 5) Medium parapodia with two papillae and a tuft of cilia. Scale bar, 10  $\mu\text{m}$ . 6) Dorsal simple seta. Scale bar, 5  $\mu\text{m}$ . 7) Compound falciger setae. Scale bar, 5  $\mu\text{m}$ . 8) Compound spiniger setae. Scale bar, 10  $\mu\text{m}$ .

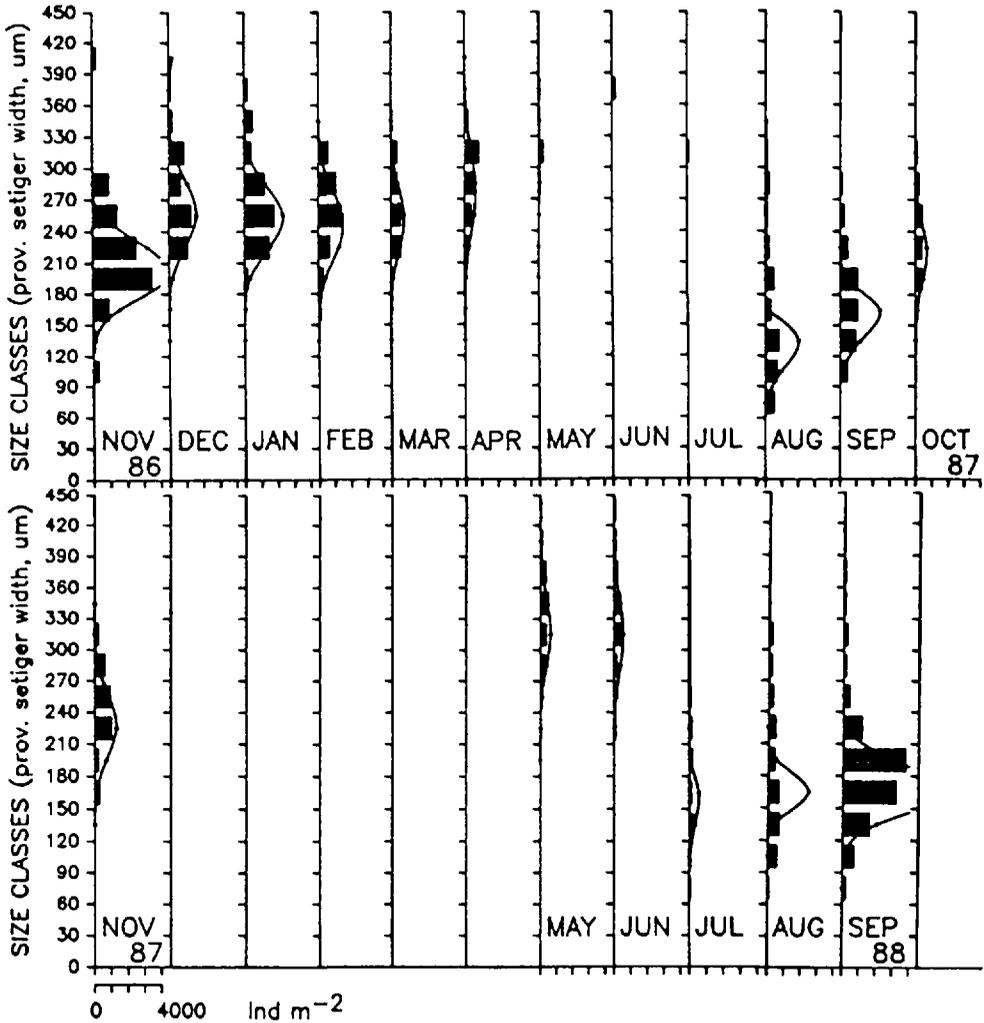


Figure 4. Size frequency histograms ( $\text{ind} \cdot \text{m}^{-2}$ ) of the *Streptosyllis verrilli* population from November 86 to September 88. No samples were obtained from December 87 to April 88. Curve lines are normalized expected frequencies.

$\mu\text{m}$  above,  $20 \mu\text{m}$  below (Figs. 2G, 3<sub>7</sub>). Single dorsal simple seta from setiger 1, thick, strongly bidentate; both teeth large, rounded, oriented in two oblique different angles; with short subdistal spines (Figs. 2D, 3<sub>6</sub>). Solitary, slender, indistinctly bifid, ventral simple seta on far posterior setigers (Fig. 2E). Pygidium subtriangular, with two anal cirri and a midventral projection or cirrus (Fig. 1B). Pharynx unarmed, short, wide, with 10 soft lobes surrounding opening, through about three segments. Proventriculus twice as long as the pharynx, extending four and a half segments, with about 55 muscle cell rows. Gut similar in width to proventriculus, usually dark green (Fig. 1A); sometimes, a slender, short ventriculus perceptible behind proventriculus.

Epitokous males with sperm from setiger 7 to setiger 26, a slender curved notoaciculum and a tuft of relatively short capillary natatory setae in each parapodium of mature segments.

*Discussion.*—*Streptosyllis verrilli* was originally placed by Moore (1907) in the genus *Syllides* Oersted, 1845. *Syllides* and *Streptosyllis* are two very similar genera (San Martín, 1984). The distinction between *Streptosyllis* and *Syllides* is based on the presence or absence of knobbed acicula in the anterior setigers. *Syllides verrilli* Moore, 1907 has these enlarged, thickened acicula from setiger 2 to setiger 6 and it must be placed in the genus *Streptosyllis*. Banse (1971) redescribed this species but he did not mention these enlarged acicula. Pettibone (1963) synonymized *Syllides verrilli* with *Syllides setosa* Verrill, 1882 which was also described from Woods Hole (Vineyard Sound) although the description of the latter species is based on sexual epitokes found in surface waters. Banse (1971) examined the Pettibone specimens and additional specimens from Buzzards Bay and recognized them to be *Syllides verrilli* but he did not mention the enlarged acicula although he mentioned the knoblike tips. Hartman (1944) published some unknown figures of Verrill (*S. setosa* is shown in plate S6, fig. 11); although there is no solitary dorsal simple seta drawn in this figure and it shows a distal tooth in its pharynx, the shape of the body and the compound setae are identical to our specimens. We examined an old microscope slide (4PM.2987) of a labelled specimen of *Syllis* sp. [= *S. setosa* Verrill?] from Woods Hole, probably a type specimen of the original collection of Verrill. The specimen is in a very bad condition and it is difficult to observe its taxonomic characteristics, especially the presence of dorsal simple seta in their parapodia. We believe that *S. setosa* and *S. verrilli* could be the same species but the lack of good descriptions of the tipus specimen of *S. setosa* does not allow us to be certain.

Ventral cirri in *Streptosyllis* are very long, broad at the bases, sometimes pseudoarticulated; ventral cirri in *Syllides* are not especially long nor pseudoarticulated. Ventral cirri of *S. verrilli* are similar to those of other species of *Streptosyllis*, as *S. websteri* Southern, 1914, *S. templadoi* San Martín, 1984 (cf. San Martín, 1984), *S. pettibonae* Perkins, 1981 (cf. Perkins, 1981), and others. Dorsal cirri of *Syllides* are usually smooth and short anteriorly, and long and articulated from setiger 3; dorsal cirri of *Streptosyllis* are rough to pseudoarticulated, as the dorsal cirri of *S. verrilli*. *Streptosyllis verrilli* shares with *S. pettibonae* the very reduced, papilliform palps, and it is the only species of the genus which combines the following characters: 1) papilliform palps, 2) dorsal cirri rough to pseudoarticulated, 3) dorsal simple setae thick, strongly bidentated, and 4) enlarged acicula from setiger 2 to setiger 6.

### Population Dynamics

*Demography and life history.*—*Streptosyllis verrilli* has an annual life cycle (Fig. 4) in the marsh. A new recruitment cohort grows during August–December and again during April–June, through these periods the cohort is subject to mortality (Fig. 5). Water temperatures and air temperatures follow a similar pattern in the Marsh (Fig. 5, top), the weather conditions seems to control the seasonal change of *Streptosyllis* populations.

During 1986–1987 mortality seemed fairly constant from fall to spring (Fig. 5, left). Monthly mean of water temperature dropped to 0°C in February 1987. This was a very cold winter, a thick layer of ice covered the channels and creeks during January and February (Fig. 5, top). Mortality occurred through the winter. The result was that very few adults of *S. verrilli* were found in the breeding season and the abundance peak of September was low. In contrast, the winter of 1988 was milder. The 1987 cohort did not suffer from a layer of ice in the sediments (average water temperature was 0.5°C) and almost 60% of the entire population

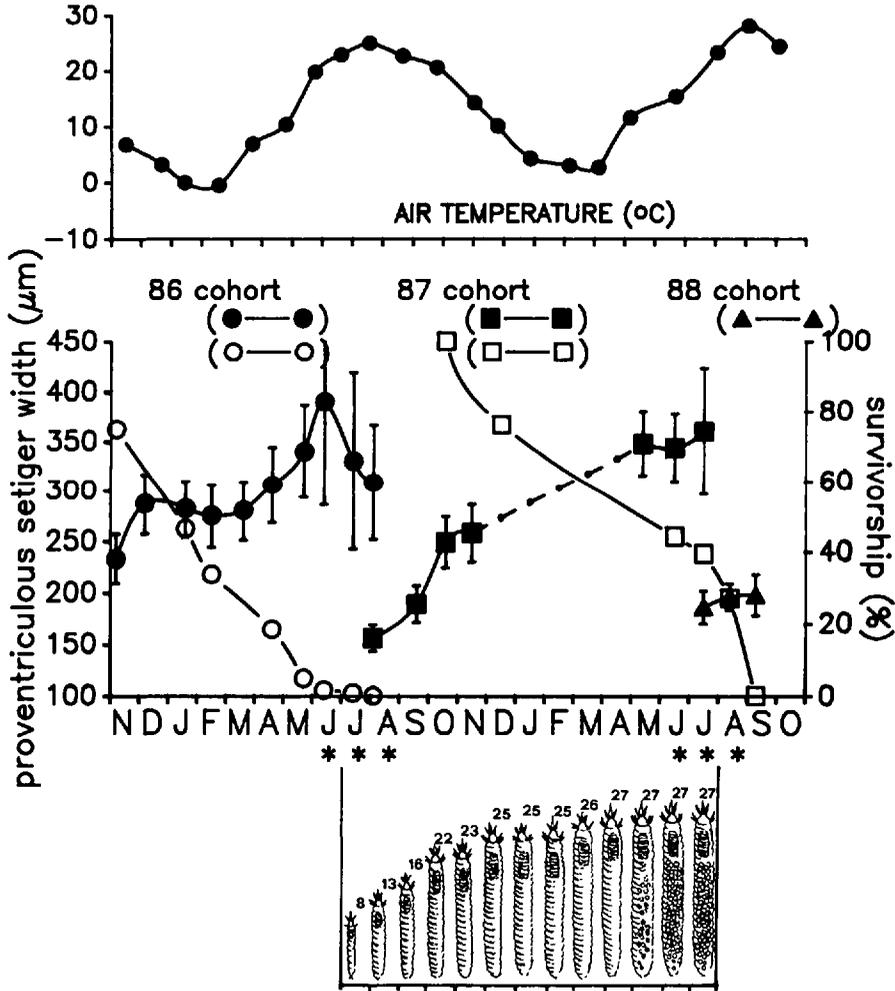


Figure 5. Left) The growth of individual year classes, in terms of increase proventriculus setiger width (Black symbols). Right) Percentage of survivorship of individual year classes (Open symbols). Air temperature data is shown at the top. Somatic and gametic growth of *Streptosyllis*, showing the setiger average by month of the population, at the bottom.

survived from December to May. Many more *S. verrilli* were present during the spring months of 1988 and presumably reproduced. As a consequence, higher recruitment peak was observed by September 1988. Perhaps in warmer winters, cold-related mortality slackens and other forms of mortality come into play. Wiltse et al. (1984) show that predation by fish during the warmer months was the major source of benthic depression. The importance of overwinter survival is that reproduction takes place in May–July, and is carried out by the survivors. Densities observed at the beginning of the sampling period, in 1986, showed that a similar pattern to the 1988 year could have happened (average water temperature in February 1986 was 0.5°C). Our survey shows that *S. verrilli* breeds only once each year in the 9th or 10th month of life, in a short spawning season as does *Odonotosyllis polycera* (Daly, 1975) but does not survive after spawning to breed again the following year. This evidence is surprising because we know that *Streptosyllis websteri*, a very similar species to *S. verrilli* breeds twice during an extended

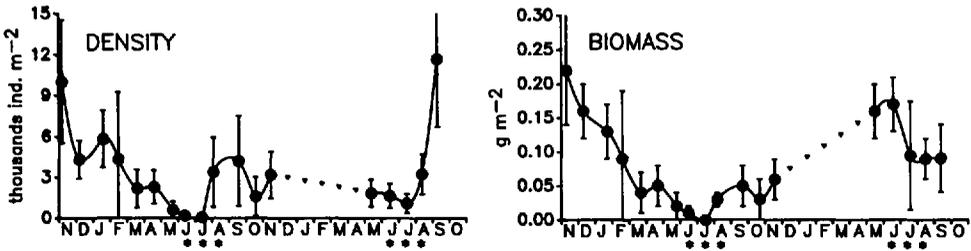


Figure 6. Density and Biomass data of *Streptosyllis verrilli* over the sampling period. No data was obtained from December '87 to April '88. The presence of asterisks in the abscissas indicates the time of the spawning season for *S. verrilli*.

spawning season in the beginning of their third year of life on the Northumberland coast, east Atlantic (Garwood, 1982). Both species have a similar ecological niche, salt marsh tidal channels for *S. verrilli* and protected tidal sand beaches for *S. websteri*. *S. verrilli* feeds mainly on diatoms and detritus. The abundance of diatoms inside the intestinal tract peaks in April–May and follows the annual cycle of diatoms and chlorophyll *a* in the Great Sippewissett marsh (Foreman, 1989). *S. verrilli* sometimes can be carnivorous, especially when diatoms are less abundant. Nematodes and copepods also were found in their intestinal tract.

**Population Size and Biomass.**—The seasonal pattern of density mirrors the life history (Fig. 6, top). Over the two years studied the average density varied from  $100 \pm 142$  individuals  $m^{-2}$  in July 1987 to  $11,707 \pm 5,000$  individuals  $m^{-2}$  in September 1988. Values around 5,000 individuals  $m^{-2}$  were reported from Wild Harbor in 1969 (Grassle and Grassle, 1974). The highest densities of *S. verrilli* were found in sandy sediments around 0.20 mm grain size with high organic content of 2 kg  $m^{-2}$  while the lowest densities were found in coarse sand with low organic content. No animals were found in muddy sediments or in exposed beach sediments. The length/frequency histograms show a clear unimodal population (Fig. 4). The abundance of the year cohort is high in fall, and diminished steadily through 1987. Very few survivors entered the reproductive season and the densities of the new cohort was much reduced relative to the previous year (compare Nov 1987 to Nov 1986, for example). In spite of this, more *S. verrilli* entered the reproductive season of 1988 than did so in 1987. Perhaps for this reason the 1988 cohort was much more abundant than the 1987 cohort (compare Sep 1988 to Sep 1987). The biomass seasonal pattern (Fig. 6, bottom) mirrors the density pattern. The biomass of *S. verrilli* peaked in November 1986 ( $0.22 \pm 0.08$  g  $m^{-2}$ ). A sharp decline in biomass of the population was observed until July 1987. By November '87 another peak was observed ( $0.06 \pm 0.03$  g  $m^{-2}$ ) but in this case values of biomass were increasing each month until June 1988 ( $0.17 \pm 0.04$  g  $m^{-2}$ ).

**Growth.**—*S. verrilli* has two main periods of growth during the year, from August to December and from March to June. During late summer and early autumn the length/frequency distribution is characterized by large numbers of smaller size groups (60–200  $\mu m$ ), which are the brood of the previous year class. By December these organisms have grown quickly to proventriculus width sizes around 270  $\mu m$ . Growth ceases during the winter season, by that time most of the animals have arrived at the maximum setiger number (26–29). From March to June growth of *S. verrilli* is done increasing biomass by gamete accumulation and undergoing gametogenesis. Animals containing gonads can be observed from May and the breeding season is restricted to the next 3 months. The cycle of growth seems to

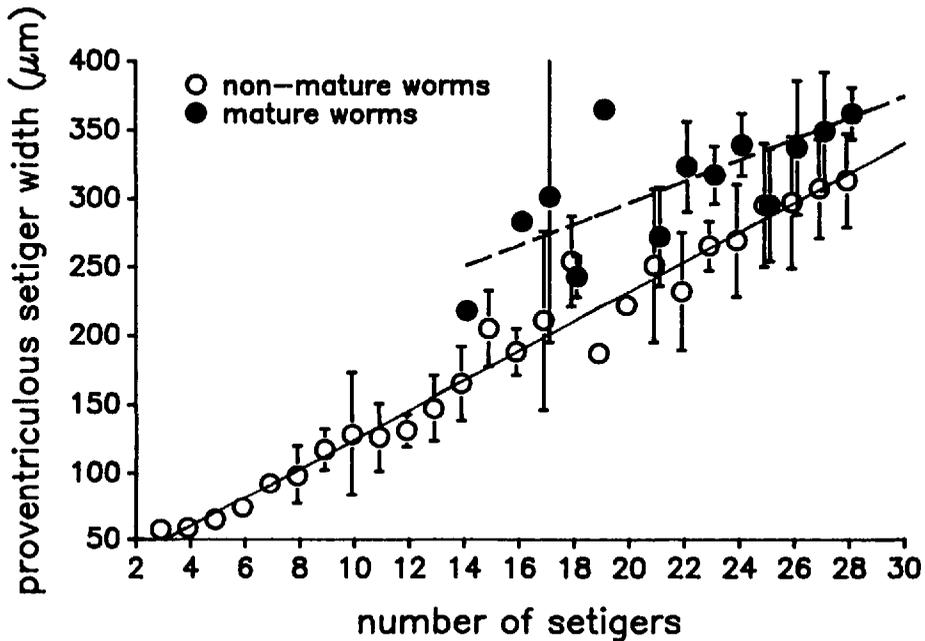


Figure 7. The relationship between proventriculus setiger width ( $y$  in  $\mu\text{m}$ ) and setiger number ( $x$ ) in *Streptosyllis verrilli* for non-mature and mature worms. Lines are linear regression;  $y = 15.683 + 10.772x$ ,  $r^2 = 0.97$  for non-mature worms, and  $y = 135.373 + 8.225x$ ,  $r^2 = 0.59$  for mature worms.

be related to two production contributions, the somatic production from August to the winter period and the gamete production from March to July (Fig. 6, bottom). Figure 7 shows the relationship between proventriculus setiger width and setiger number comparing immature individuals with mature individuals. From March to June growth results from accumulation of gametes. About 24% of the total production was in the form of gametic production during the second year of the study (the first year was very cold and most of the adult population crashed during the winter period).

*Production.*—Mean annual biomass for the *Streptosyllis* population was 0.07 g dry wt  $\text{m}^{-2}$  during November '86 to October '87 and 0.13 g dry wt  $\text{m}^{-2}$  during November '87 to October '88 (average of 0.10 g dry wt  $\text{m}^{-2}$ ). We estimated secondary production by two independent methods. A first estimate of secondary production was obtained by summing increases in biomass that occurred from one sampling date to the next (Table 1). Production during November 86 to October 87 was 0.19 g dry wt  $\text{m}^{-2}$  while production during November 87 to October 88 was 0.47 g dry wt  $\text{m}^{-2}$ . This estimate of production is undoubtedly low because it ignores losses of biomass produced between sampling dates. P/B values obtained in this way were 2.83 for the first year and 3.71 for the second year (average of  $3.27 \pm 0.44$ ). A second estimate of production was calculated using the relationship of Banse and Mosher (1980) between mean adult size and P/B ratio. Mean adult size (270.8  $\mu\text{m}$ ) or biomass (0.02086 mg), obtained from specimens that had reached maximum size, was converted to caloric equivalent (Ms) using the taxon specific energy contents (col. B) given in Brey et al. (1988). Estimates of the annual P/B ratio were calculated from the equation

$$\text{P/B} = 0.64 \cdot \text{Ms}^{-0.37} \text{ (Banse and Mosher, 1980)}$$

Table 1. Summary of data used in the calculation of the mean annual biomass, annual production and P/B ratio. (\*) We estimate production during November 1986 using the same ratio registered from October 1987 to November 1987

Monthly sample	Abundance N·m <sup>-2</sup>	Biomass g·m <sup>-2</sup>	Production	
1986 November	10,049	0.21 (*)	0.14	Nov 86–Oct 87
December	4,329	0.15		
1987 January	5,828	0.13		Mean annual biomass
February	4,236	0.09		0.07 g m <sup>-2</sup>
March	2,210	0.04		Production
April	2,311	0.05	0.01	0.19 g m <sup>-2</sup>
May	603	0.02		
June	201	0.01		P/B ratio = 2.83
July	100	0.01		
August	3,417	0.02	0.01	
September	4,221	0.05	0.03	
October	1,608	0.02		
November	3,216	0.06	0.04	Nov 87–Oct 88
December	—	0.078		
1988 January	—	0.096		
February	—	0.114		Mean annual biomass
March	—	0.132		0.13 g m <sup>-2</sup>
April	—	0.150		Production
May	1,865	0.17	0.11	0.47 g m <sup>-2</sup>
June	1,661	0.12		P/B ratio = 3.71
July	1,110	0.03		
August	3,273	0.10	0.07	
September	11,710	0.35	0.25	

The obtained P/B ratio (20.65) was then multiplied by the average biomass observed during the two years studied (Table 1) to obtain production. For very small invertebrates, mass scaled estimates of P/B ratios computed in this fashion may be too high (Banse, 1982) and provide an upper limit on production. These estimates were seven times higher than those calculated by summing increases in biomass occurring over the season, 1.44 g m<sup>-2</sup> for 1987 and 2.68 g m<sup>-2</sup> for 1988. The values of the P/B found in this study,  $3.27 \pm 0.44$ , are intermediate in the range of values published for marine benthic polychaetes (Sanders, 1956; Kay and Brafield, 1973; Buchanan and Warwick, 1974; Warwick and Price, 1975; Wolf and de Wolf, 1977; Cederwall, 1977; Warwick et al., 1978; Ménard et al., 1989; Ambroggi, 1991; Gillet, 1990), although there is no data for syllid species due to their small size and difficulties to sampling. Warwick (1979) show the relationship between maximum life span and P/B, the regression line obtained by Warwick goes to values around three for annual species.

#### ACKNOWLEDGMENTS

We most gratefully acknowledge Dr. N. W. Riser, for his observations and discussion. We acknowledge Salt Pond Sanctuaries and D. and the late A. Gifford for use of their land. We acknowledge P. Polloni, associated researcher of the Gray Museum (Marine Biological Laboratory of Woods Hole, Massachusetts), for the loan of Moore specimens of *Syllides verrilli* and for her useful comments. We thank the Microscopical Service of the University of Barcelona for assistance with the scanning pictures. A Fulbright Postdoctoral grant supported R. Sardá during this work.

#### LITERATURE CITED

- Ambroggi, R. 1991. Secondary production of *Prionospio caspersi* (Annelida: Polychaeta: Spionidae). Mar. Biol. 104: 437–442.

- Banse, K. 1971. A new species, and additions to the description of six other species of *Syllides* Oersted (Syllidae: Polychaeta). *J. Fish. Res. Board Canada* 28(10): 1469–1481.
- . 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. *Mar. Ecol. Prog. Ser.* 9: 281–297.
- and S. Mosher. 1980. Adult body mass and annual production/biomass relationships in field populations. *Ecol. Monogr.* 50: 355–379.
- Brey, T., H. Rumohr and S. Ankar. 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *J. Exp. Mar. Biol. Ecol.* 117: 271–278.
- Buchanan, J. B. and R. M. Warwick. 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. *J. Mar. Biol. Assoc. U.K.* 54: 197–222.
- Cederwall, H. 1977. Annual macrofauna production on a soft bottom in the northern Baltic proper. Pages 155–164 in B. F. Keegan, P. O. Ceidigh and P. J. S. Boaden, eds. *Biology of benthic organisms*.
- Daly, J. M. 1975. Reversible epitoky in the life history of the polychaete *Odontosyllis polycera* (Schmarda, 1861). *J. Mar. Biol. Assoc. U.K.* 55: 327–344.
- Foreman, K. H. 1989. Regulation of benthic microalgal and meiofaunal productivity and standing stock in a salt marsh ecosystem: the relative importance of resources and predation. Ph.D. thesis, Boston University. 200 pp.
- Franke, H. D. 1980. Zur Determination der zeitlichen Verteilung von Fortpflanzungsprozessen in Laborkulturen des Polychaeten *Typosyllis prolifera*. *Helgolander Meeresuntersuchungen* 34: 61–84.
- Garwood, P. 1982. The life-cycle and population dynamics of *Streptosyllis websteri* (Polychaeta: Syllidae) from a Northumberland Beach. *J. Mar. Biol. Assoc. U.K.* 62: 783–798.
- . 1991. Reproduction and the classification of the family Syllidae (Polychaeta). *Ophelia Suppl.* 5: 81–87.
- Gillet, P. 1990. Biomasse, production et dynamique des populations de *Nereis diversicolor* (annélide polychète) de l'estuaire de la Loire (France). *Oceanologica Acta* 13(3): 361–372.
- Grassle, J. F. and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. Mar. Res.* 32: 253–284.
- Hartman, O. 1944. New England Annelida. Part 2. Including the unpublished plates by Verrill with reconstructed captions. *Bull. Amer. Mus. Nat. Hist.* 82(7): 327–344, pls. 45–60.
- Kay, D. G. and A. E. Brafield. 1973. The energy relations of the polychaete *Neanthes* (= *Nereis*) *virens* (Sars). *J. Anim. Ecol.* 42: 673–692.
- Ménard, F., F. Gentil and J. C. Dauvin. 1989. Population dynamics and secondary production of *Owenia fusiformis* Delle Chiaje (Polychaeta) from the Bay of Seine (eastern English Channel). *J. Exp. Mar. Biol. Ecol.* 133: 151–167.
- Michael, A. D., C. R. Van Raalte and L. S. Brown. 1975. Long-term effects of an oil spill at West Falmouth, Massachusetts, in 1975 Conference on Prevention and Control of Oil Pollution, Proceedings, March 25–27, 1975, San Francisco. American Petroleum Institute, Washington, D.C. Pp. 573–582.
- Moore, J. P. 1907. Description of a new species of annelid from Woods Hole. *Proc. Acad. Nat. Sc. Phil.* 5: 448–451.
- Perkins, T. H. 1981. Syllidae (Polychaeta), principally from Florida, with descriptions of a new genus and twenty-one new species. *Proc. Biol. Soc. Wash.* 93(4): 1080–1172.
- Pettibone, M. H. 1963. Marine polychaete worms of the New England region 1. Aphroditidae through Trochochaetidae. *U.S. Nat. Mus. Bull.* 227: 1–356.
- Sanders, H. L. 1956. Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. *Bull. Bingham Oceanogr. Coll.* 15: 345–414.
- , J. F. Grassle, G. R. Hampson, L. S. Morse, S. Garner-Price and C. C. Jones. 1980. Anatomy of an oil spill: long term effects from the grounding of the barge *Florida* off West Falmouth, Massachusetts. *J. Mar. Res.* 38(2): 265–380.
- San Martín, G. 1984. Estudio biogeográfico, faunístico y sistemático de los Poliquetos de la familia Silidos (Polychaeta: Syllidae) en Baleares. Ed. de la Universidad Complutense de Madrid. Ph.D. thesis, Madrid. 529 pp.
- Sardá, R., K. Foreman and I. Valiela. In Press. Controls of benthic invertebrate populations and production of salt marsh tidal creeks: experimental enrichment and short and long term effects. *Proc. 26th E.M.B.S.*
- Warwick, R. M. 1979. Population dynamics and secondary production of benthos. Pages 1–24 in K. R. Tenore and B. C. Coll, eds. *Marine benthic dynamics*.
- and R. Price. 1975. Macrofauna production in an estuarine mud-flat. *J. Mar. Biol. Assoc. U.K.* 55: 1–18.
- , C. L. George and J. R. Davis. 1978. Annual macrofauna production in a *Venus* community. *Est. Coastl. Mar. Sci.* 7: 215–241.

- Whitlatch, R. B. 1977. Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barnstable Harbor, Massachusetts. *Biol. Bull.* 152: 275–294.
- Wiltse, W. I., K. H. Foreman, J. H. Teal and I. Valiela. 1984. Effects of predators and food resources on the macrobenthos of salt marsh creeks. *J. Mar. Res.* 42: 923–942.
- Wolf, W. J. and L. de Wolf. 1977. Biomass and production of zoobenthos in the Grevelingen estuary, the Netherlands. *Est. Coastl. Mar. Sci.* 5: 1–24.

DATE ACCEPTED: December 10, 1991.

ADDRESSES: (R.S.) *Boston University Marine Program, Marine Biological Laboratory, Woods Hole, 02543 Massachusetts*; PRESENT ADDRESS: *Centro de Estudios Avanzados de Blanes, (C.S.I.C.). Camino de Santa Barbara s/n. 17300 Blanes (Gerona), Spain*; (G.S.M.) *Universidad Autónoma de Madrid, Dpto. Zoología. Ciudad Universitaria Canto Blanco, 28049 Madrid, Spain.*